

**BIOLOGY AND IMMATURE STAGES OF EIGHT SPECIES OF  
LAUXANIIDAE (DIPTERA). II. DESCRIPTIONS OF  
IMMATURE STAGES AND DISCUSSION OF LARVAL  
FEEDING HABITS AND MORPHOLOGY**

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ABSTRACT—The morphology of the eggs, 3 larval instars, and puparia of *Camptoprosopella confusa* Shewell, *Homoneura americana* (Wiedemann), *Lyciella browni* (Curran), *Minettia lupulina* (Fabricius), *M. lyraformis* Shewell, *Poecilominettia ordinaria* (Melander), *Pseudocalliope flaviceps* (Loew), and *Pseudogriphoneura gracilipes* (Loew) are described and illustrated. The significance of the larval feeding habits and of the morphology of the larvae is discussed.

The first part of this study (Miller and Foote, 1975) presented life history information and observations on larval food preferences for *Camptoprosopella confusa* Shewell, *Homoneura americana* (Wiedemann), *Lyciella browni* (Curran), *Minettia lupulina* (Fabricius), *M. lyraformis* Shewell, *Poecilominettia ordinaria* (Melander), *Pseudocalliope flaviceps* (Loew), and *Pseudogriphoneura gracilipes* (Loew), 8 species of lauxaniid flies that are common and widely distributed in eastern North America.

The present paper includes descriptions and illustrations of the eggs, 3 larval instars, and puparia of these same 8 species. It also discusses the significance of the larval feeding habits and of the morphology of the larvae.

DESCRIPTIONS OF IMMATURE STAGES

Several features held in common by the 8 species studied in this investigation are presented below. In the individual species descriptions given later, only the third instars are described in detail; descriptions of the 2 earlier instars are restricted to distinctive characters.

Egg: White. Micropyle apical, shielded dorsally by small tubercle. Ends of eggs reticulated or pitted, without ridges. Elsewhere, chorion with few to numerous longitudinal ridges.

First Instar: White to colorless, integument transparent to translucent. Malpighian tubules white, usually inconspicuous. Metapneustic. Facial mask with at most 2 indistinct rows of spinules. Two spiracular slits, forming V-shaped structure. Cephalopharyngeal skeleton usually lightly pigmented and weakly developed; basal part of mouthhooks lacking windows; no dental sclerites; epistomal sclerite apparently fused to hypostomal sclerite; posteroventral margin of hypo-

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stomal sclerite fused with anterior border of pharyngeal sclerite, hypostomal bridge poorly developed; ligulate sclerites barely noticeable; posterior margins of ventral cornua of pharyngeal sclerite poorly defined, no parastomal bars, pharyngeal ridges in floor of pharyngeal sclerite indistinct.

Second Instar: Malpighian tubules white, usually evident. Facial mask with 3-4 rows of distinct spinules. Cephalopharyngeal skeleton deeply pigmented; mouthhooks with hook part and ventromedial portion of basal part less pigmented; hypostomal sclerite fused to pharyngeal sclerite; pharyngeal ridges 6-8.

Third Instar: White, integument translucent. Conic-cylindrical, usually tapering more anteriorly than posteriorly, somewhat flattened. Malpighian tubules white, conspicuous, convoluted, located between cephalopharyngeal skeleton and mid-point of body. All segments with spinule bands on anterodorsal margins, segments 3-12 with spinule bands also on anteroventral margins.

Segment 1 longitudinally bilobed apically; each lobe bearing short and fleshy 2-segmented antenna and unsegmented maxillary palp, palp without distinct sclerotized basal ring; facial mask with 4 or 5 distinct rows of spinules, most anteroventral spinules not in rows, spinules somewhat darkened and bifurcate apically.

Anterior spiracles white; located posterolaterally on segment 2; each spiracle with few to many apical papillae, each papilla surrounded by membrane; spiracles commonly projecting at nearly right angles to body of larva. Segment 12 with protrusible ambulatory lobes arising from the elongate-oval perianal pad on venter; anal slit elongate, in middle of perianal pad; posterior spiracular tubes generally arising close together on posterodorsal surface of spiracular disc; spiracular disc with variously placed marginal lobes and tubercles. Posterior spiracular plates at apices of frequently darkened spiracular tubes, each plate with 3 spiracular slits, 4 variously branched interspiracular processes, and 1 oval spiracular scar.

Cephalopharyngeal skeleton mostly deeply pigmented. Mouthhooks well developed, converging anteriorly, not fused dorsally, hook part strongly decurved (except in *Lyciella browni*), basal part with 2 small, nearly contiguous windows medially (except in *Camptoprosopella confusa*). Dental sclerites well developed (except in *Minettia lyraformis* and *Lyciella browni*), triangular in lateral view and linear in ventral view. Epistomal sclerite arched; with rod-like rami posteriorly extending to near middle of hypostomal sclerite, rami parallel and mesad parastomal bars. Hypostomal sclerite generally H-shaped, not fused posteriorly to pharyngeal sclerite, no hypostomal plate. Subhypostomal sclerites paired, linear, located anterior to ventral bridge of hypostomal sclerite. Ligulate sclerites paired, each articulating with 1 subhypostomal sclerite, sclerites converging anteriorly and usually connected apically by thin membrane. Pharyngeal sclerite with anterodorsal bridge connecting anterior ends of dorsal cornua; anterior edge of pharyngeal sclerite underriding posterior edge of hypostomal sclerite; parastomal bars slender, arising from anterior margin of pharyngeal sclerite and ending laterad to epistomal sclerite; each ventral cornu with window of varying size and shape near posterodorsal margin (except in *Camptoprosopella confusa*, which lacks windows); floor of sclerite with 9 pharyngeal ridges.

Puparium: Integument more or less covered by calcareous, whitish secretion (except in *Pseudocalliope flaviceps*); puparium itself translucent, anterior end slightly flattened dorsoventrally forming lateral ridges. Facial mask black (ex-

cept in *P. flaviceps*). Anterior spiracles anterolaterad on 1st apparent segment; marginal papillae varying in shape and number, usually white. Ambulatory lobes around perianal pad retracted. Spinule bands as in 3rd instar.

*Camptoprosopella confusa* Shewell, 1939

Egg (fig. 1): Length 0.62–0.66 mm, greatest width 0.23–0.27 mm. Ovoid, more convex dorsally than ventrally; anterior end gradually narrowing to broad tubercle shielding micropyle dorsally; posterior end narrowing to small, round tubercle borne on slightly constricted stalk. Chorionic ridges 11–13, undivided or occasionally branching posteriorly.

First Instar: Length 1.00–1.78 mm, greatest width 0.23–0.40 mm. Posterior spiracular plates (fig. 67) with numerous long, finely branched interspiracular processes with 3–4 branches. Cephalopharyngeal skeleton (fig. 27) length 0.18–0.21 mm; mouthhooks well developed, hook part with accessory tooth.

Second Instar: Length 1.41–3.22 mm, greatest width 0.37–0.61 mm. Anterior spiracles (fig. 11) with apical papillae short. Spiracular plates (fig. 74) with longer interspiracular processes. Cephalopharyngeal skeleton length 0.28–0.31 mm; hook part of mouthhooks (fig. 34) with 1 accessory tooth.

Third Instar: Length 3.01–5.18 mm, greatest width 0.56–1.05 mm. Prominent spinule bands on anterodorsal and anteroventral margins of segments, less prominent rows of spinules elsewhere on segments. Anterior spiracles (fig. 15) fan-shaped, with 5–7 finger-like, apical papillae. Segment 12 (fig. 93) ventrally with small pointed ambulatory lobes, posterior end of anal slit with cluster of 7–12 spinules; spiracular disc (fig. 90) with pair of small and pointed dorsolateral tubercles, pair of large and blunt lateral tubercles, and pair of small and blunt ventrolateral tubercles; spiracular plate (fig. 82) with 5- or 6-branched interspiracular processes.

Cephalopharyngeal skeleton (fig. 49–52) length 0.43–0.48 mm. Basal part of mouthhooks broad, with 2 small faint, widely separated windows (fig. 50). Epistomal sclerite narrow, posterior rami free apically (fig. 52). Hypostomal sclerite with narrow bridge (fig. 51). Ligulate sclerites much shorter than subhypostomal sclerites (fig. 51). Pharyngeal sclerite (fig. 49) deeply pigmented; anterodorsal bridge broad and indented anteromedially, with numerous oval windows anteriorly and laterally and faint windows centrally (fig. 52); dorsal cornua tapered posteriorly, slightly shorter than ventral cornua; ventral cornua without windows, somewhat rounded apically and with short linear spur extending posterodorsally; parastomal bars apparently fusing distally to dorsomedial surface of hypostomal sclerite.

Puparium (fig. 109): Length 2.45–3.36 mm, greatest width 0.98–1.40 mm. Shiny, light yellow to light orange. Elongate oval, more convex dorsally than ventrally, broadest at mid-length in dorsal view; posterior end rounded, about as broad as anterior end. Perianal pad depressed below general surface of puparium, with light brown transverse groove. Anterior spiracles sessile, with 5–7 marginal papillae.

*Homoneura americana* (Wiedemann), 1830

Egg (fig. 2): Length 0.58–0.73 mm, greatest width 0.23–0.32 mm. Ovoid; anterior end pointed and bearing small tubercle dorso-apically, posterior end more rounded; chorion with 11–13 undivided or rarely branching ridges, ridges con-



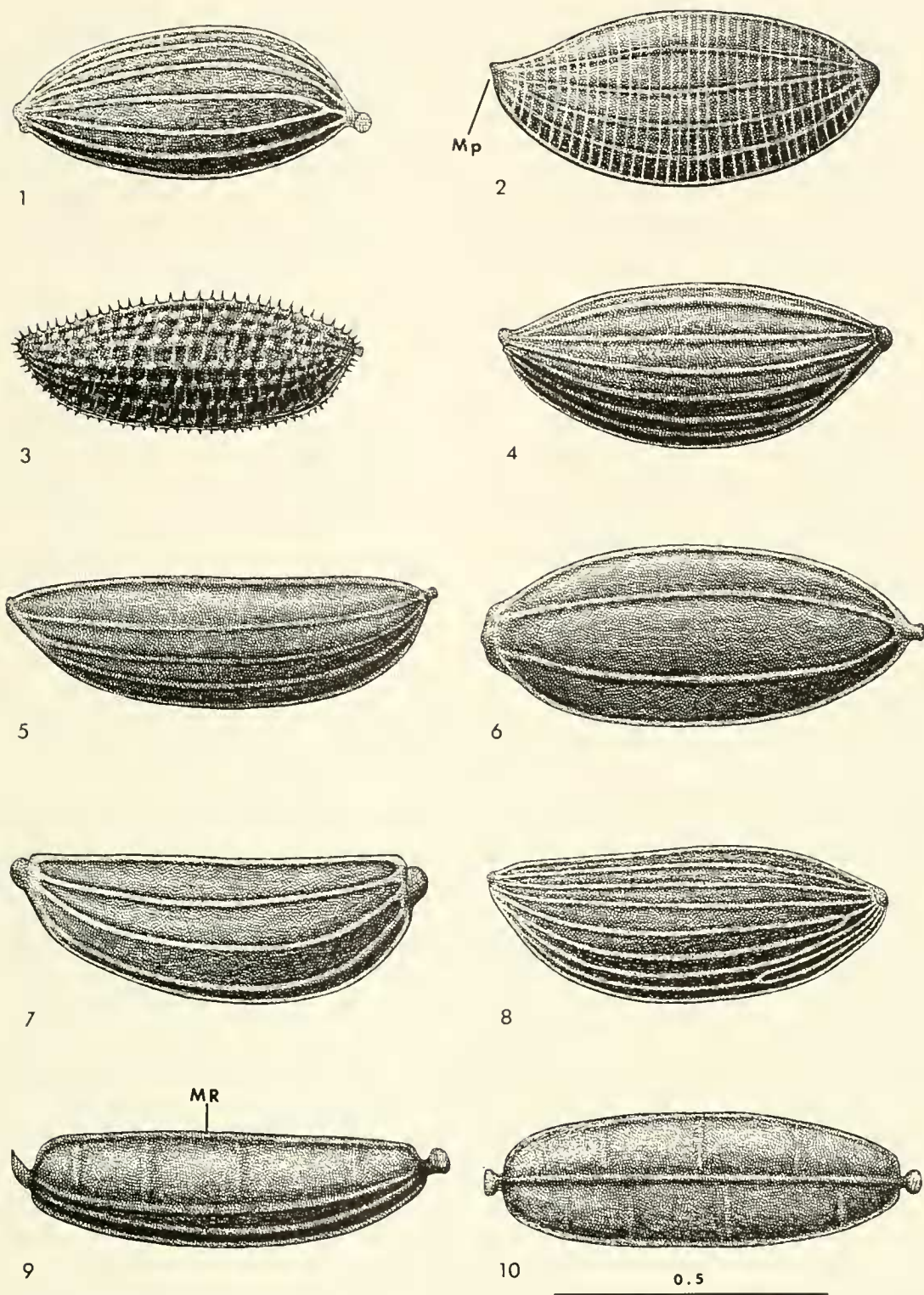


Fig. 1-10. Eggs. 1, *C. confusa*. 2, *H. americana*. 3, *L. browni*. 4, *M. lupulina*. 5, *M. lyraformis*. 6, same, dorsal view. 7, *P. ordinaria*. 8, *P. flaviceps*. 9, *P. gracilipes*. 10, same, dorsal view.

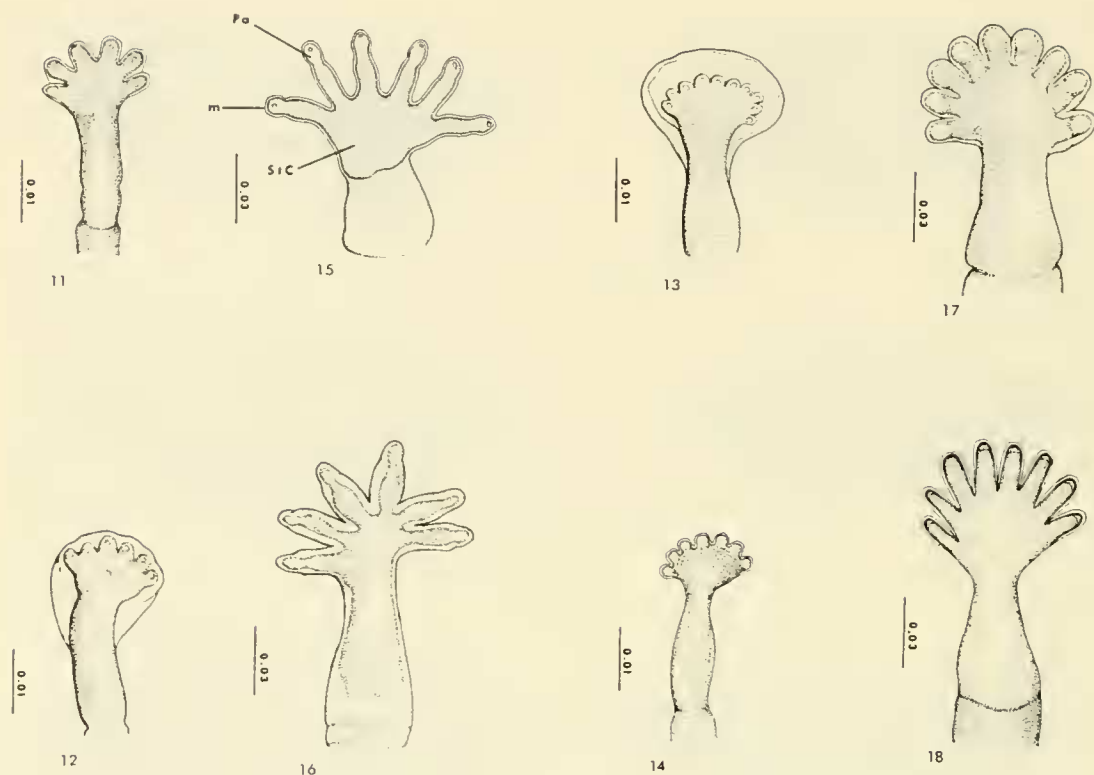


Fig. 11-18. Anterior spiracles. 11-14, 2nd instars. 15-18, 3rd instars. 11, 15, *C. confusa*. 12, 16, *H. americana*. 13, 17, *L. browni*. 14, 18, *M. lupulina*.

ected by faint transverse septae, 8-10 dorsal ridges more conspicuous than ventral ridges.

First Instar: Length 0.87-1.84 mm, greatest width 0.20-0.34 mm. Posterior spiracular plates (fig. 71) with 4 or 5 branched interspiracular processes, hairs composing processes not branching apically. Cephalopharyngeal skeleton (fig. 31) length 0.19-0.21 mm; mouthhooks with large accessory tooth laterad on tip and small tooth posteriorly; posterior portion of basal parts narrow, weakly sclerotized.

Second Instar: Length 2.03-3.12 mm, greatest width 0.35-0.66 mm. Spiracles (fig. 12) with 5-6 very short apical papillae. Spiracular plates (fig. 78) with longer interspiracular processes. Cephalopharyngeal skeleton length 0.35-0.41 mm; mouthhooks (fig. 38) with hook part bearing large accessory tooth arising from side of hook and faint accessory tooth close to base of hook.

Third Instar (Fig. 102-104): Length 2.91-3.52 mm, greatest width 1.11-1.33 mm. Prominent spinule bands on anterodorsal and anteroventral margins of segments; spinule bands less conspicuous elsewhere. Anterior spiracles (fig. 16) somewhat fan-shaped, with 5-8 finger-like papillae. Segment 12 (fig. 94) ventrally with very short, pointed ambulatory lobes arising from perianal pad; spiracular disc (fig. 91) with pair of blunt dorsolateral tubercles and pair of blunt 2-tipped, lateral tubercles; spiracular plates (fig. 86) with interspiracular processes having 5-7 branches, some branches bifurcating apically.

Cephalopharyngeal skeleton (fig. 53-55) length 0.53-0.63 mm. Hook part of mouthhooks with small accessory tooth; basal part with anterior window about twice as large as posterior window (fig. 53). Epistomal sclerite narrow, arched

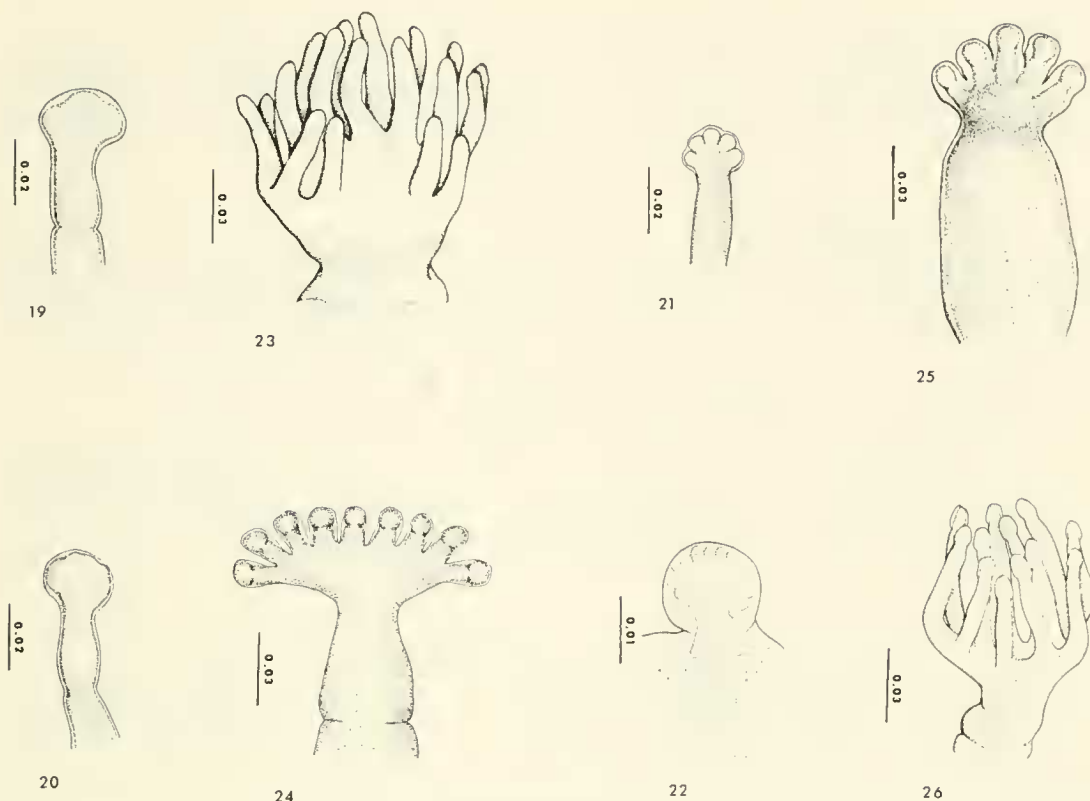


Fig. 19–26. Anterior spiracles. 19–22, 2nd instars. 23–26, 3rd instars. 19, 23, *M. lyraformis*. 20, 24, *P. ordinaria*. 21, 25, *P. flaviceps*. 22, 26, *P. gracilipes*.

dorsally. Hypostomal sclerite distinctly H-shaped, bridge arched ventrally (fig. 54). Ligulate sclerites linear, about same length and shape as subhypostomal sclerites (fig. 54). Pharyngeal sclerite less pigmented anterodorsally, with broad bridge; bridge (fig. 55) poorly pigmented medially and without windows; dorsal cornua heavily pigmented on ventral margin, slightly longer than ventral cornua; ventral cornua poorly pigmented ventrally and posteriorly, pigmented dorsal margin extending posteriorly as narrow black line (fig. 53). Parastomal bars entirely free from hypostomal sclerite.

Puparium (fig. 105, 106): Length 2.91–3.52 mm, greatest width 1.10–1.33 mm. Dull, light yellow to light orange. Elongate oval, slightly more convex dorsally; strongly tapering posteriorly; posterior end distinctly pointed. Perianal pad somewhat protruding. Anterior spiracles sessile, base of expanded portion black.

#### *Lyciella browni* (Curran), 1933

Egg (fig. 3): Length 0.62–0.69 mm, greatest width 0.23–0.29 mm. Ovoid; anterior end slightly narrowed to broad tubercle that shields micropyle dorsally; posterior end bearing very small, round tubercle apically. Longitudinal ridges 22–30, mostly not branching; dorsal ridges more prominent and not branching, bearing large, projecting spines at regular intervals; very faint ventral ridges occasionally bifurcating and bearing spines  $\frac{1}{3}$  size of spines on more dorsal ridges.

First Instar: Length 1.07–1.94 mm, greatest width 0.23–0.44 mm. Spiracular plates (fig. 68) with 3–5-branched interspiracular processes. Cephalopharyngeal skeleton (fig. 30) length 0.20–0.23 mm; only tip of mouthhooks sclerotized; epi-



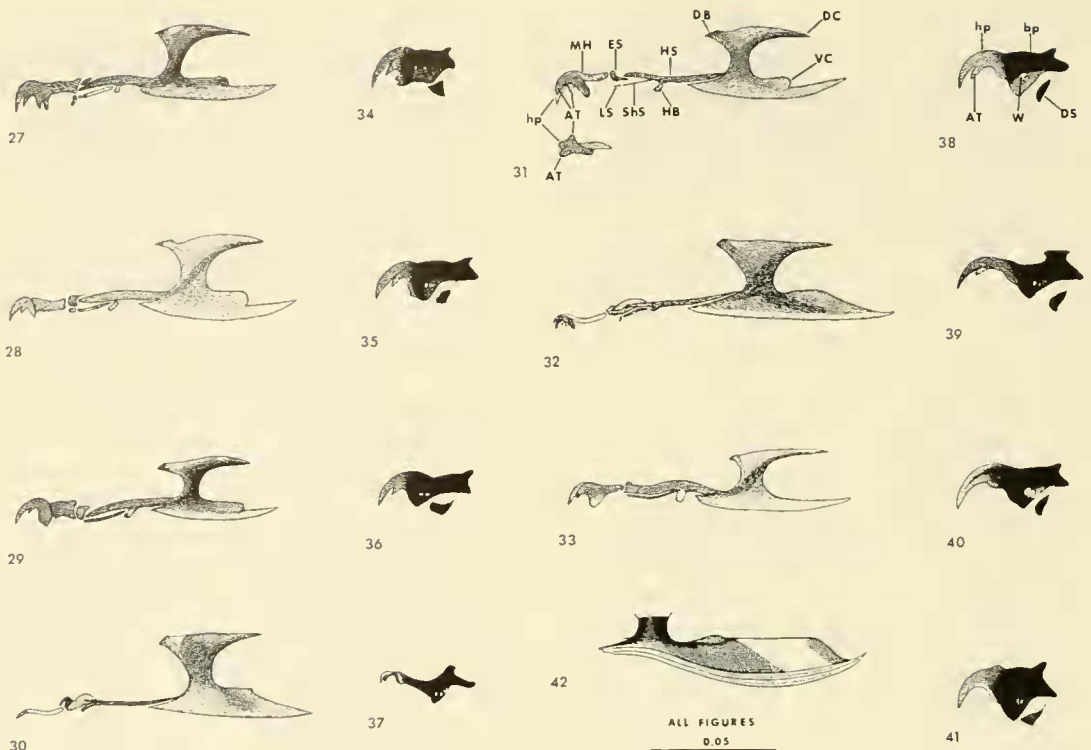


Fig. 27-33. Cephalopharyngeal skeletons of 1st instars. Fig. 34-41. Left mouthhooks of 2nd instars. 27, 34, *C. confusa*. 28, 35, *M. lupulina*. 29, 36, *P. gracilipes*. 30, 37, *L. browni*. 31, 38, *H. americana*. 32, 39, *M. lyraformis*. 33, 40, *P. flaviceps*. 41, *P. ordinaria*. Fig. 42. *L. browni*, ventral cornu of pharyngeal sclerite of 2nd instar.

stomal sclerite appearing to have small hook anteromedially on bridge; pharyngeal sclerite poorly sclerotized.

Second Instar: Length 1.82-3.85 mm, greatest width 0.42-0.91 mm. Anterior spiracles (fig. 13) with very short papillae apically. Posterior spiracular plates (fig. 75) with 3-5-branched, rather broad interspiracular processes. Cephalopharyngeal skeleton length 0.45-0.50 mm; mouthhooks (fig. 37) with hook part bearing accessory tooth nearly equal to length of hook tip, tooth arising from side of hook part; dental sclerites absent; ventral cornua (fig. 42) with hyaline parallelogram-shaped area near posterior end.

Third Instar: Length 3.50-5.43 mm, greatest width 0.70-1.19 mm. Integument with very large spinules not in distinct rows, spinules covering entire dorsal and lateral surfaces of all segments; anteroventral margin of each segment also with narrow band of small spinules. Anterior spiracles (fig. 17) fan-shaped, with 9-10 relatively short, apical papillae. Perianal pad with long, narrow, and tapering ambulatory lobes. Margin of spiracular disc (fig. 98) with pair of small dorsolateral tubercles; very small lateral tubercles; and pair of large, pointed ventrolateral tubercles. Spiracular plates (fig. 83) with 7 to 9-branched interspiracular processes.

Cephalopharyngeal skeleton (fig. 43-45) length 0.80-0.92 mm. Hook part of each mouthhook slightly decurved, mesally with faint window above small accessory tooth; basal part with anterior window slightly larger than posterior window (fig. 43). Epistomal sclerite broad, arched dorsally (fig. 45). Hypostomal sclerite

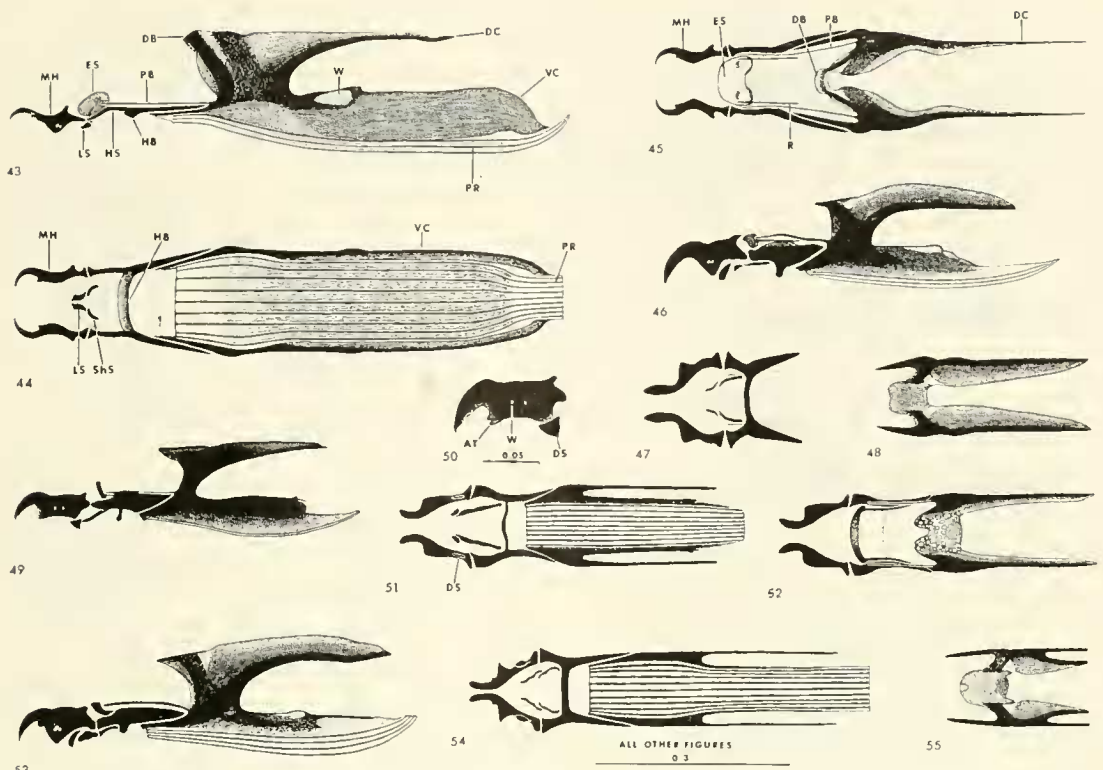


Fig. 43–55. Cephalopharyngeal skeleton of 3rd instars. 43, *L. browni*, lateral view. 44, same, ventral view. 45, same, dorsal view. 46, *M. lupulina*, lateral view. 47, same, ventral view of mouthhooks and hypostomal sclerite. 48, same, dorsal view of pharyngeal sclerite. 49, *C. confusa*, lateral view. 50, same, left mouthhook. 51, same, ventral view of cephalopharyngeal skeleton. 52, same, dorsal view. 53, *H. americana*, lateral view. 54, same, ventral view. 55, same, dorsal view of pharyngeal sclerite.

elongate, bridge narrow and arched ventrally (fig. 44). Subhypostomal sclerites slightly longer than ligulate sclerites. Pharyngeal sclerite narrowly bridged anterodorsally, bridge (fig. 45) without windows; dorsal cornua very narrow, shorter than broad ventral cornua; ventral cornua heavily pigmented only around large basodorsal window, strongly and abruptly narrowed apically to small tip. Parastomal bars free.

Puparium (fig. 110): Length 3.22–3.57 mm, greatest width 1.26–1.47 mm. Dull chestnut brown to dark brown to almost black. Elongate, semihemispherical in lateral view; strongly convex dorsally, flattened ventrally, tapering posteriorly from 4A; posterior end slightly flattened dorsally forming lateral ridges on segments 10 to 12. Posterior spiracles directed upward. Anterior spiracles sessile. Perianal pad depressed, dark brown to black.

*Minettia lupulina* (Fabricius), 1787

Egg (fig. 4): Length 0.68–0.76 mm, greatest width 0.26–0.31 mm. Ovoid; anterior end bearing small pointed tubercle, posterior end more rounded. Longitudinal ridges 12–16, running singly or occasionally bifurcating; ends of egg faintly reticulated.

First Instar: Length 0.94–2.01 mm, greatest width 0.26–0.40 mm. Posterior spiracular plates (fig. 73) with very long, branching interspiracular processes.



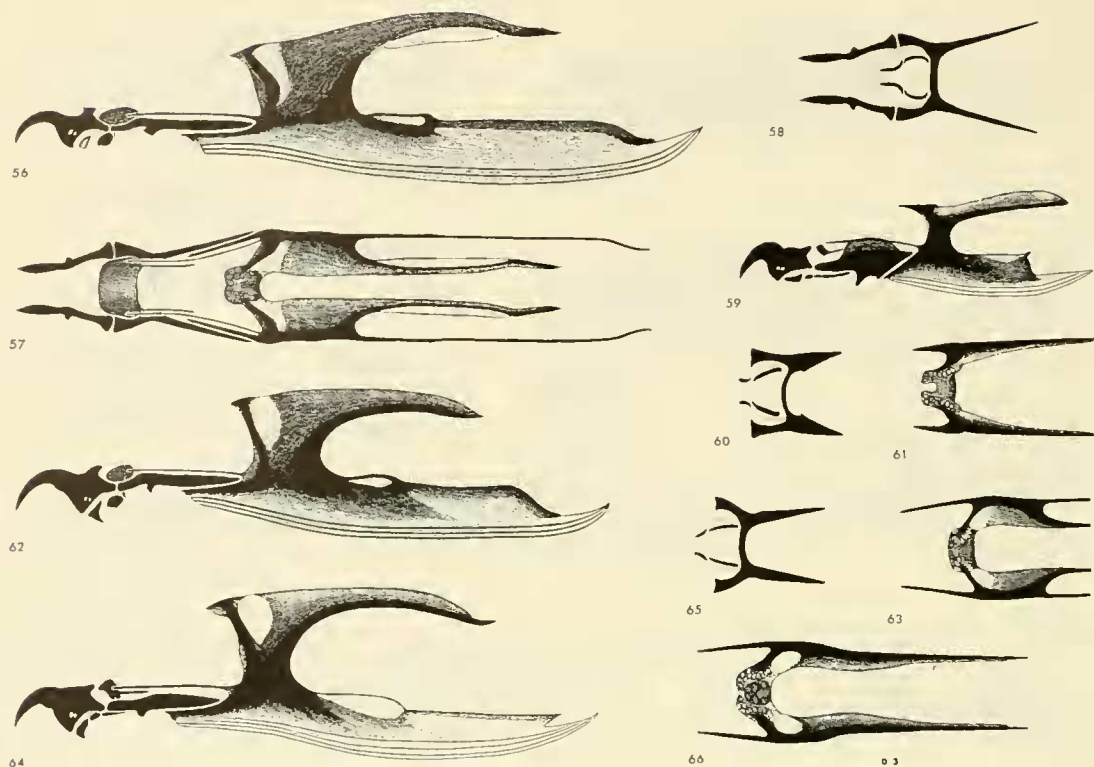


Fig. 56-66. Cephalopharyngeal skeleton of 3rd instars. 56, *M. lyraformis*, lateral view. 57, same, dorsal view. 58, same, ventral view of mouthhooks and hypostomal sclerite. 59, *P. gracilipes*, lateral view. 60, same, ventral view of hypostomal sclerite. 61, same, dorsal view of pharyngeal sclerite. 62, *P. ordinaria*, lateral view. 63, same, dorsal view of pharyngeal sclerite. 64, *P. flaviceps*, lateral view. 65, same, ventral view of hypostomal sclerite. 66, same, dorsal view of pharyngeal sclerite.

Cephalopharyngeal skeleton (fig. 28) length 0.19-0.22 mm; weakly pigmented except for broad line on pharyngeal sclerite. Mouthhooks with small accessory tooth posterior from hook tip; anteroventral margin of basal part tooth-like.

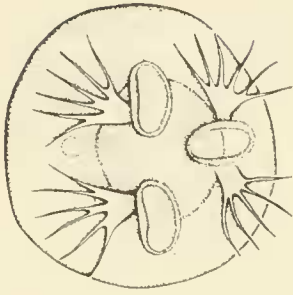
Second Instar: Length 1.68-3.22 mm, greatest width 0.42-0.63 mm. Anterior spiracles (fig. 14) with short, bluntly rounded apical papillae. Posterior spiracular plates (fig. 80) with 3 or 4-branched interspiracular processes. Cephalopharyngeal skeleton length 0.30-0.35 mm. Mouthhooks (fig. 35) with hook part bearing large accessory tooth.

Third Instar: Length 2.94-5.95 mm, greatest width 0.70-1.40 mm. Large spinules in distinct bands on anterodorsal and anteroventral margins, bands of minute spinules elsewhere on dorsal and ventral surfaces of segments.

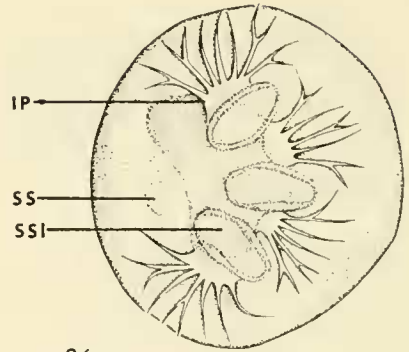
Anterior spiracles (fig. 18) fan-shaped, with 5-9 apical papillae. Ambulatory lobes of perianal pad long and pointed. Posterior spiracular disc (fig. 97) with pair of small dorsolateral tubercles and pair of large, more pointed ventrolateral tubercles. Posterior spiracular plates (fig. 88) with many interspiracular processes bifurcating apically.

Cephalopharyngeal skeleton (fig. 46-48) length 0.51-0.60 mm. Basal part of mouthhook with 2 equal-sized windows (fig. 46). Epistomal sclerite broad and arched dorsally. Hypostomal sclerite relatively short and broad (fig. 47); lateral rami of epistomal sclerite appearing to fuse with more lightly pigmented area

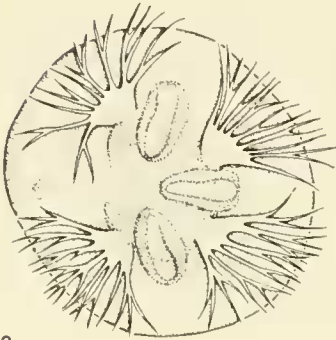




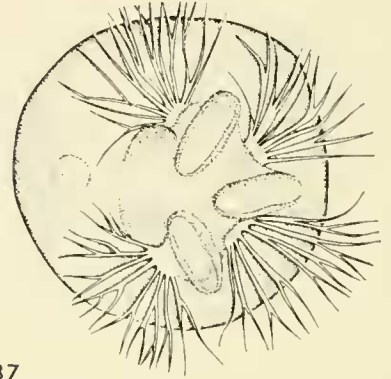
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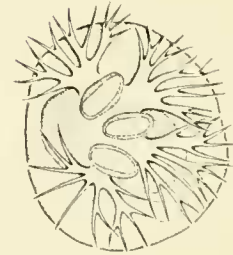
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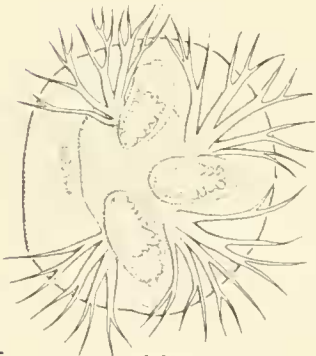
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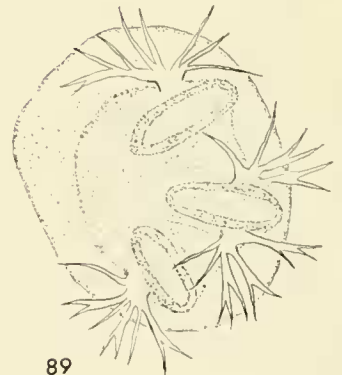
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ALL OTHER FIGURES

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Fig. 82-89. Posterior spiracular plates of 3rd instars. 82, *C. confusa*. 83, *L. browni*. 84, *P. flaviceps*. 85, *P. gracilipes*. 86, *H. americana*. 87, *M. lyraformis*. 88, *M. lupulina*. 89, *P. ordinaria*.



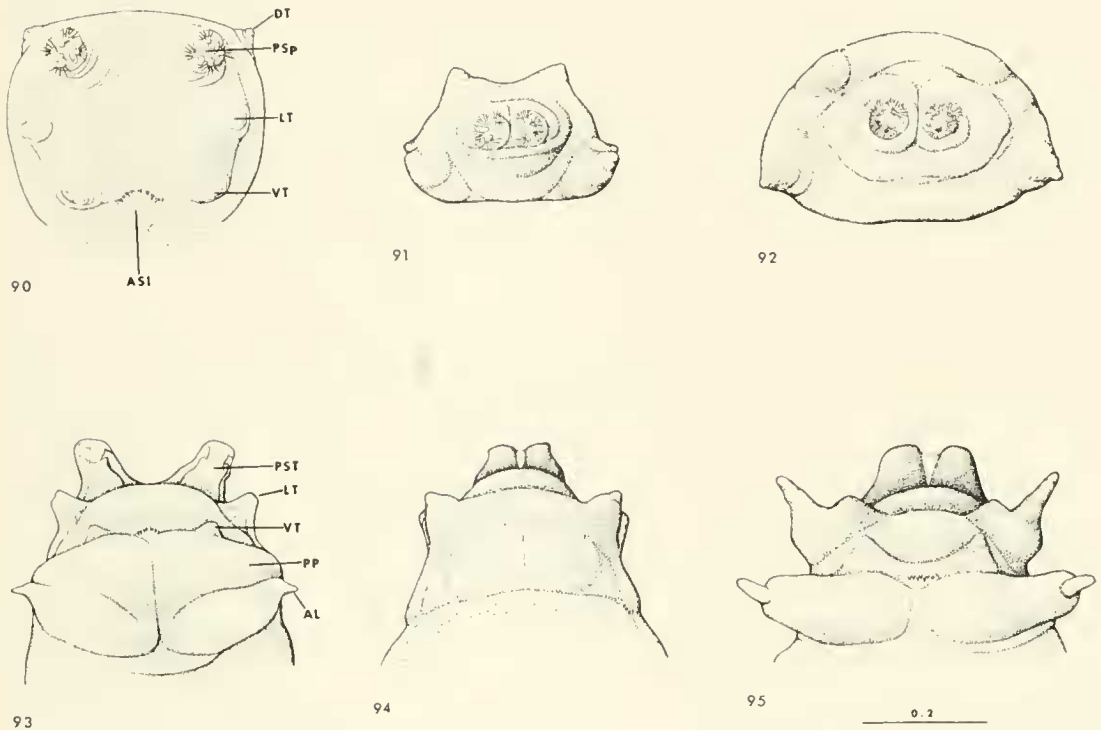


Fig. 90-92. Posterior spiracular discs of 3rd instars. Fig. 93-95. Ventral view of posterior ends of 3rd instars. 90, 93, *C. confusa*. 91, 94, *H. americana*. 92, 95, *M. lyraformis*.

dorsad from hypostomal sclerite. Ligulate sclerites about  $\frac{1}{2}$  length of subhypostomal sclerites (fig. 47). Pharyngeal sclerite broadly bridged anterodorsally; bridge with slight indentation anteromedially, without windows (fig. 48); dorsal cornua heavily pigmented on ventral margin, shorter than ventral cornua; ventral cornua pigmented lightly around small dorsal window, sometimes with additional smaller window immediately posterior to larger one, cornua somewhat flaring and upturned apically (fig. 46). Parastomal bars free from hypostomal sclerite.

Puparium (fig. 115, 116): Length 3.01-3.99 mm, greatest width 1.19-1.75 mm. Shiny red orange to red brown. Elongate oval, strongly convex dorsally, flattened ventrally, abruptly tapering posteriorly, posterior end pointed. Anterior spiracles sessile. Perianal pad depressed.

*Minettia lyraformis* Shewell, 1938

Egg (fig. 5, 6): Length 0.76-0.84 mm, greatest width 0.20-0.27 mm. Elongate oval, somewhat convex ventrally and flattened dorsally; anterior end slightly narrowed, bearing broad tubercle; posterior end bearing small round tubercle on slightly narrowed, short stalk. Chorion with 6-8 undivided longitudinal ridges; 4 dorsal ridges very prominent and with broad grooves; 2-4 lateral ridges less prominent and closer together; occasionally with very faint indications of 2 additional ridges on ventral surface.

First Instar: Length 1.04-1.71 mm, greatest width 0.23-0.34 mm. Posterior spiracular plates (fig. 72) with finely branched interspiracular processes. Cephalopharyngeal skeleton (fig. 32) length 0.25-0.30 mm. Mouthhooks very poorly developed, somewhat resembling spinules on facial mask; hook part apparently

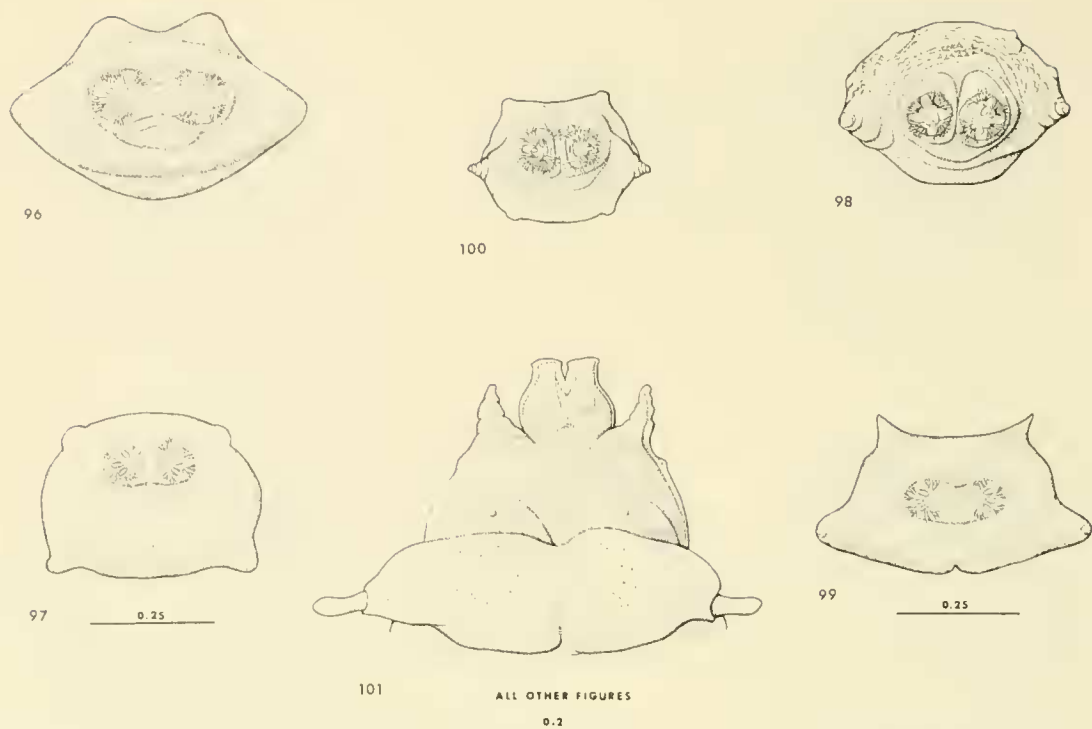


Fig. 96–100. Posterior spiracular discs of 3rd instars. 96, *P. ordinaria*. 97, *M. lupulina*. 98, *L. browni*. 99, *P. flaviceps*. 100, *P. gracilipes*. Fig. 101. *P. gracilipes*, ventral view of posterior end.

with 3 accessory teeth, 1 tooth extending beyond tip of hook, posterior portion of basal part reduced and barely pigmented. Hypostomal sclerite appearing weakly bridged anteriorly. Ventral cornua of pharyngeal sclerite tapering posteriorly.

Second Instar: Length 1.68–4.34 mm, greatest width 0.49–0.77 mm. Anterior spiracles (fig. 19) clubshaped, with 3 broadly rounded areas apically. Posterior spiracular plates (fig. 79) with interspiracular processes broad basally. Cephalopharyngeal skeleton length 0.49–0.56 mm. Mouthhooks (fig. 39) with hook part bearing very small accessory tooth. Dental sclerites subtriangular.

Third Instar: Length 4.20–7.14 mm, greatest width 0.84–1.75 mm. All segments with large spinule bands on anterodorsal and anteroventral margins; spinule bands less prominent bands elsewhere.

Anterior spiracles (fig. 23) handshaped, with 14–19 finger-like papillae. Segment 12 (fig. 95) ventrally with ambulatory lobes elongate and narrow; with 6–10 spinules behind anal slit. Posterior spiracular disc (fig. 92) bearing pair of pointed dorsolateral tubercles and pair of somewhat smaller, pointed ventrolateral tubercles. Posterior spiracular plates (fig. 87) with elongate, multibranching interspiracular processes, processes bifurcating apically.

Cephalopharyngeal skeleton (fig. 56–58) length 0.95–1.04 mm. Basal part of each mouthhook with anterior window twice as large as posterior window (fig. 56). Dental sclerites indistinct and poorly pigmented. Epistomal sclerite broad and arched dorsally (fig. 57). Ligulate sclerites approximately same length as subhypostomal sclerites (fig. 58). Hypostomal sclerite elongate, with narrow ventral bridge, posterior rami about twice as long as anterior rami (fig. 58). Pharyngeal sclerite with broad anterodorsal bridge, bridge slightly indented an-

teriorly and with numerous oval windows having pigmented spots (fig. 57); ventral cornua heavily pigmented only around window and along dorsal edge.

Puparium (fig. 113, 114): Length 3.50–4.27 mm, greatest width 1.54–2.03 mm. Shiny red orange or red brown to almost black. Elongate hemispherical in lateral view, convex dorsally and flattened ventrally; abruptly tapering posteriorly, posterior end somewhat pointed. Posterior spiracles directed upward. Anterior spiracles sessile. Perianal pad depressed, with black transverse groove.

*Poecilominettia ordinaria* (Melander), 1913

Egg (fig. 7): Length 0.68–0.79 mm, greatest width 0.23–0.27 mm. Elongate oval, strongly convex posteroventrally, flattened dorsally; anterior end slightly narrowing and bearing round tubercle; posterior end more rounded, bearing slightly larger and rounder tubercle. Longitudinal ridges 8–10, ridges undivided.

Second Instar: Length 1.65–3.65 mm, greatest width 0.32–0.75 mm. Anterior spiracles (fig. 20) clubshaped, without apical papillae. Posterior spiracular plates (fig. 81) with broad, branching interspiracular processes. Cephalopharyngeal skeleton length 0.37–0.44 mm. Mouthhooks (fig. 41) with hook part having very slight indication of unpigmented accessory tooth. Dental sclerite heavily pigmented, triangular.

Third Instar: Length 3.50–4.90 mm, greatest width 0.70–1.02 mm. Integument with large spinules in more or less distinct bands on all segments, no bands medially on dorsal and ventral surfaces, spinules on anterodorsal and ventral margins slightly larger.

Anterior spiracles (fig. 24) broadly fan-shaped, with 8–11 apical papillae. Segment 12 ventrally with large, cylindrical ambulatory lobes; posterior end of anal slit with 6–9 spinules. Posterior spiracular disc (fig. 96) bearing pair of large, blunt dorsolateral tubercles and larger pair of lateral tubercles. Posterior spiracular plates (fig. 89) with 3 to 6-branched interspiracular processes, some processes bifurcating apically.

Cephalopharyngeal skeleton (fig. 62, 63) length 0.79–0.89 mm. Hook part of mouthhooks with very slight indication of accessory tooth; basal part with 2 equal-sized windows (fig. 62). Epistomal sclerite broad. Hypostomal sclerite narrow, with broad ventral bridge. Ligulate sclerites shorter than subhypostomal sclerites. Pharyngeal sclerite with broad anterodorsal bridge having numerous elongate-oval windows laterally (fig. 63); ventral cornua heavily pigmented around large window, with narrow band of pigment on dorsal margin extending well beyond tip of dorsal cornua, abruptly tapered apically (fig. 62).

Puparium (fig. 111): Length 2.94–3.85 mm, greatest width 1.25–1.68 mm. Dull, mostly clay colored, anterior and posterior ends black. Elongate ovoid, convex dorsally and flattened ventrally; tapering posteriorly, posterior end pointed. Anterior spiracles sessile, black basally. Perianal pad somewhat depressed, with brown median slit.

*Pseudocalliope flaviceps* (Loew), 1866

Egg (fig. 8): Length 0.70–0.81 mm, greatest width 0.23–0.33 mm. Ovoid, more convex ventrally; anterior end pointed and bearing small tubercle, posterior end more rounded. Longitudinal ridges 20–26, not or only occasionally bifurcating.

First Instar: Length 0.72–0.81 mm, greatest width 0.27–0.34 mm. Posterior spiracular plates (fig. 69) with few-branched interspiracular processes, processes



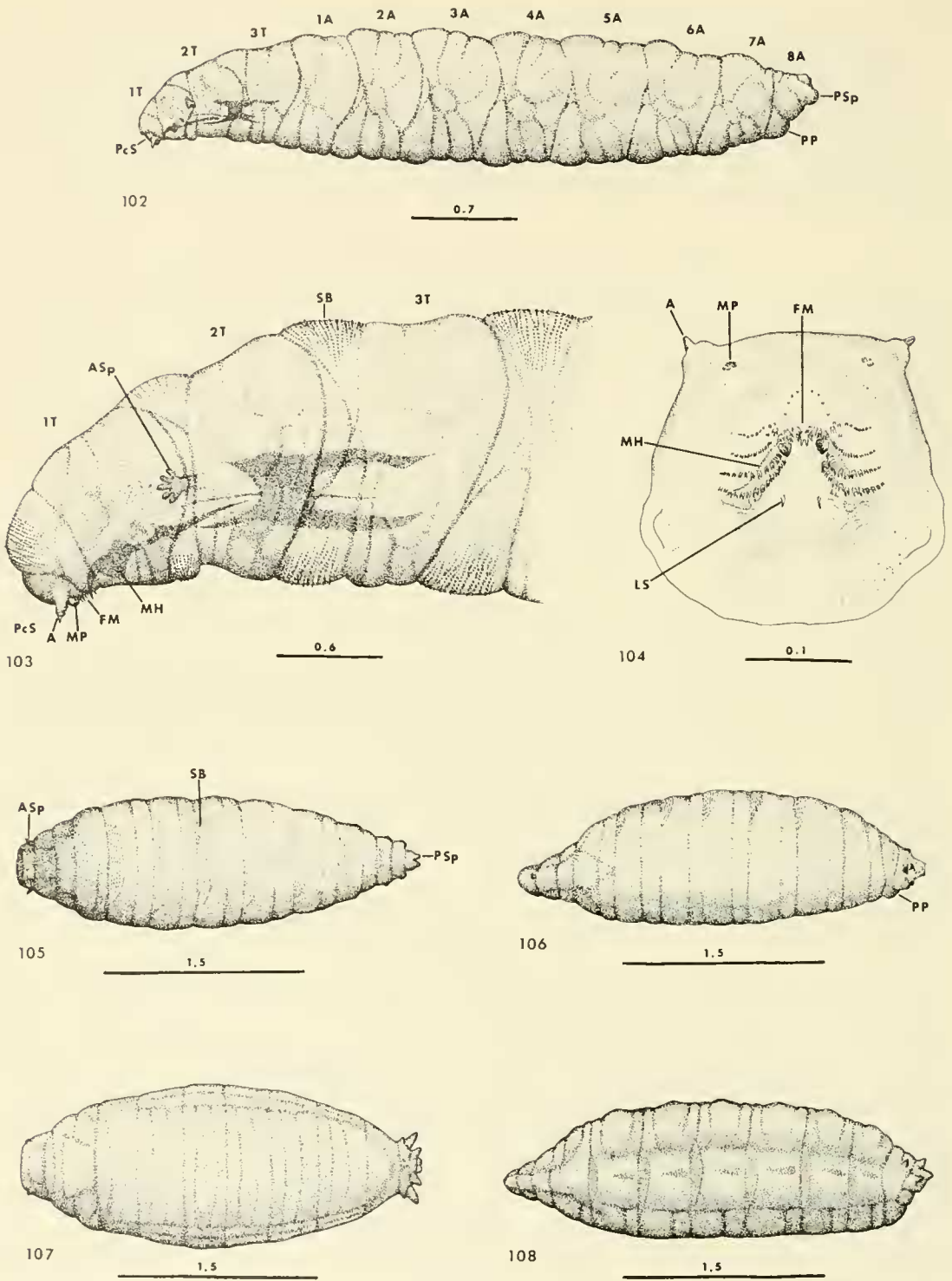


Fig. 102-106. *H. americana*. 102, habitus of 3rd instar. 103, lateral view of anterior end of 3rd instar. 104, ventral view of segment 1. 105, puparium, dorsal view. 106, same, lateral view. Fig. 107-108. *P. flaviceps*. 107, puparium, dorsal view. 108, same, lateral view.

rarely bifurcating apically; spiracular slits narrow and elongate. Cephalopharyngeal skeleton (fig. 33) length 0.20–0.25 mm; weakly pigmented. Mouthhooks with hook part bearing small accessory tooth; anteroventral area of basal part very lightly pigmented. Epistomal sclerite strongly fused to hypostomal sclerite. Ventral cornua of pharyngeal sclerite very lightly pigmented, posterior margin indistinct.

Second Instar: Length 1.40–4.36 mm, greatest width 0.25–0.63 mm. Anterior spiracles (fig. 21) with 4–6 short, bud-like papillae. Posterior spiracular plates (fig. 76) with broad, 3 or 4-branched interspiracular processes. Cephalopharyngeal skeleton length 0.40–0.49 mm. Mouthhooks (fig. 40) with slight indication of accessory tooth on base of hook part.

Third Instar: Length 3.95–5.32 mm, greatest width 0.70–1.33 mm. Integument with large spinules not in distinct bands on anterodorsal and anteroventral margins of all segments; small spinules in distinct rows elsewhere.

Anterior spiracles (fig. 25) elongate with 5–6 relatively broad papillae apically; segment 12 ventrally with elongate, cylindrical, apically blunt ambulatory lobes; posterior end of anal slit with 5–8 spinules. Posterior spiracular disc (fig. 99) bearing pair of slender, pointed dorsolateral tubercles and 2 very large, blunt ventrolateral tubercles. Posterior spiracular plates (fig. 84) with short, few-branched interspiracular processes; spiracular slits elongate, each slit with small circular structures apically.

Cephalopharyngeal skeleton (fig. 64–66) length 0.75–0.84 mm; rather weakly pigmented. Hook part of mouthhooks with very slight indication of accessory tooth; basal part with anterior window nearly twice as large as posterior window (fig. 64). Epistomal sclerite broad and arched dorsally. Hypostomal sclerite with narrow ventral bridge (fig. 65). Ligulate sclerites shorter than subhypostomal sclerites (fig. 65). Pharyngeal sclerite with broad anterodorsal bridge, bridge slightly indented anteromedially, with numerous elongate-oval windows anteriorly and laterally and faint, large oval windows centrally (fig. 66); ventral cornua lightly pigmented, with very large window basodorsally.

Puparium (fig. 107, 108): Length 2.81–4.55 mm, greatest width 1.12–2.03 mm. Shiny light yellow to light brown. Elongate oval, with lateral ridges; somewhat convex dorsally and slightly flattened ventrally; posterior end rounded, as wide as anterior end, with noticeable tubercles around spiracular disc. Facial mask not blackened. Anterior spiracles white, slightly projecting. Perianal pad slightly depressed.

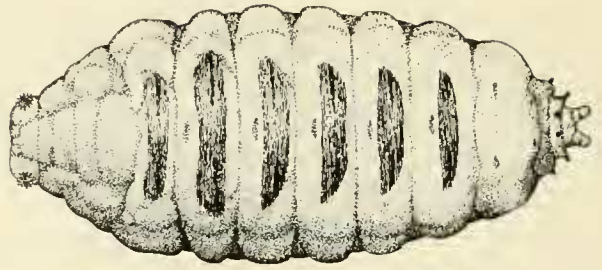
*Pseudogriphoneura gracilipes* (Loew), 1861

Egg (fig. 9, 10): Length 0.75–0.84 mm, greatest width 0.16–0.23. Elongate oval, flattened dorsally and slightly convex ventrally; anterior end more rounded and bearing elongate, apically flattened tubercle; posterior end slightly narrowing and bearing round tubercle on narrow, short stalk. Chorion with 5–7 undivided longitudinal ridges; egg on each side of middorsal ridge with 3–4 widely separated transverse septae; lateral ridges 4–6, close together, ventralmost pair indistinct.

First Instar: Length 0.87–1.71 mm, greatest width 0.23–0.37 mm. Posterior spiracular plates (fig. 70) with long several-branched interspiracular processes, spiracular slits with elongate structures apically. Cephalopharyngeal skeleton



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113



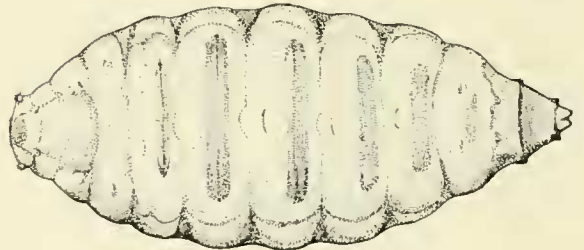
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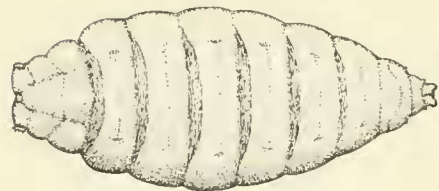
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Fig. 109-116. Puparia. 109, *C. confusa*, dorsal view. 110, *L. browni*, dorsal view. 111, *P. ordinaria*, dorsal view. 112, *P. gracilipes*, dorsal view. 113, *M. lyriformis*, dorsal view. 114, same, lateral view. 115, *M. lupulina*, dorsal view. 116, same, lateral view.



(fig. 29) length 0.17–0.19 mm; rather heavily pigmented. Mouthhooks well developed; hook part bearing small accessory tooth; basal part robust.

Second Instar: Length 1.75–3.15 mm, greatest width 0.42–0.63 mm. Anterior spiracles (fig. 22) somewhat fanshaped, with 12–15 short apical papillae. Posterior spiracular plates (fig. 77) with elongate many-branched interspiracular processes. Cephalopharyngeal skeleton length 0.28–0.33 mm. Mouthhooks (fig. 36) with hook part less heavily pigmented, bearing slender accessory tooth.

Third Instar: Length 3.08–5.32 mm, greatest width 0.63–1.12 mm. Integument with small spinules forming bands on anterodorsal and anteroventral margins of each segment, remainder of each segment devoid of conspicuous spinules.

Anterior spiracles (fig. 26) handshaped, with 11–14 finger-like papillae, each papilla slightly swollen apically. Segment 12 ventrally (fig. 101) with rather elongate ambulatory lobes. Posterior spiracular disc (fig. 100) bearing pair of small dorsolateral tubercles, pair of more elongate lateral tubercles, and 2 blunt ventrolateral tubercles. Posterior spiracular plates (fig. 85) with elongate spiracular scars, spiracular slits oval, with small round structures apically and short trabeculae laterally. Interspiracular processes multibranched and bifurcating apically.

Cephalopharyngeal skeleton (fig. 59–61) length 0.48–0.53 mm; deeply pigmented. Basal part of mouthhook with 2 equal-sized windows (fig. 59). Epistomal sclerite rather narrow; posterior rami free. Hypostomal sclerite with narrow ventral bridge, posterior rami very broad near bridge (fig. 60). Ligulate sclerites shorter than subhypostomal sclerites (fig. 60). Anteroventral projection of pharyngeal sclerite short (fig. 59); anterodorsal bridge broad and deeply indented anteromedially, with oval windows laterally (fig. 61); dorsal cornua with faint window posterodorsally; ventral cornua only slightly longer than dorsal cornua, each cornu with short spur dorsoposteriorly. Parastomal bars fused to lighter pigmented area of hypostomal sclerite.

Puparium (fig. 112): Length 2.73–3.50 mm, greatest width 1.10–1.41 mm. Shiny light yellow to light orange. Elongate oval, convex dorsally and flattened ventrally; anterior end with pronounced indentation medially; tapering posteriorly, posterior end distinctly pointed. Anterior spiracles sessile. Perianal pad somewhat depressed, with brown median slit.

#### DISCUSSION

According to Oldroyd (1964), the Lauxaniidae have retained the ancestral acalyptrate habit of feeding on such compostlike material as vegetable debris. Our rearings support this assumption, although it is probable that the larvae are actually ingesting such microorganisms as fungi, yeasts, and bacteria. Dowding (1967) has described the structure and function of the longitudinal ridges that are so prominent in the floor of the pharyngeal sclerite of saprophagous cyclorraphous Diptera larvae, stating that these ridges constitute a filtering mechanism that separates particulate matter from a semi-liquid medium. Cross sections of lauxaniid larvae that we have studied clearly show pharyngeal ridges.

At least 2 lines of specialization have evolved among the saprophagous Lauxaniidae. One group, represented by *Homoneura americana*

and *Minettia lupulina*, has become adapted to feeding as miners within the decaying mesophyll tissues of fallen leaves. A second group, including *Pseudocalliope flaviceps* and *Poecilominettia ordinaria*, have become specialized for utilizing decaying material found in birds' nests. Although larvae of 2 species were found in leaf litter, it was not determined whether each species was segregating onto different food resources. However, our rearings do indicate that larvae of one species at least prefer certain kinds of deciduous tree leaves over others. Thus, larvae of *Homoneura americana* completed development on a diet of sugar maple (*Acer saccharum* Marshall) and wild black cherry (*Prunus serotina* Ehrhart) leaves and were able to reach the third instar on American elm (*Ulmus americana* L.) and alder (*Alnus* sp.) leaves. In contrast, they failed to feed on decaying leaves of white oak (*Quercus alba* L.) and American beech (*Fagus grandifolia* Ehrhart). Possibly the high tannin content of the oak and beech leaves deterred feeding (Feeney, 1970). Larvae of other species seemed to prefer decaying leaves of maple, alder, and cherry, but much more testing is necessary before any valid conclusions as to segregation of larval feeding preferences can be drawn. There is also the possibility that larvae occupying the same microhabitat (e.g., leaf litter) are actually utilizing different microorganisms such as yeasts, fungi, and bacteria and thus avoid competition. Preference for different kinds of yeasts, for example, seems to be a common phenomenon in species of Drosophilidae (Lindsay, 1958; Wagner, 1944).

It is probable that the Lauxaniidae are the North American ecological homologues of the leaf-feeding species of Hawaiian Drosophilidae (Heed, 1968). In contrast to the Hawaiian drosophilids, however, the leaf-feeding Lauxaniidae do not seem to show a reduction in numbers of eggs produced (Kambysellis and Heed, 1971) and probably are best considered as being r-strategists (MacArthur and Wilson, 1967).

The two birds' nests species were not studied carefully enough to allow many generalizations, although there is some indication that these species have a lowered fecundity compared to the leaf-mining forms. Thus, females of *Pseudocalliope flaviceps* deposited less than 70 eggs each and this species may be a K-strategist (MacArthur and Wilson, 1967). In contrast, females of *Minettia lyraformis*, a leaf-feeding species, commonly produced nearly 500 eggs. Immature stages of the birds' nest-inhabiting species occasionally were found in the same nest during mid-summer months, but it is not known whether their larvae were competing for the same food resource. *Pseudocalliope flaviceps* overwinters as mature larvae or pupae, whereas *Poecilominettia ordinaria* apparently passes the winter as an adult. Possibly the larval feeding stages of the two species are separated in time.

Because so few lauxaniid eggs and larvae have been studied, it is

impossible at this time to characterize the family or genera morphologically. In general, the mature larvae are rather typically muscoidan, although there has been some flattening of the body dorsoventrally. The most conspicuous character held in common by all of the second and third-stage larvae investigated is the pair of large white glands that appear to be extensions of the Malpighian tubules. These structures apparently store calcium carbonate and are most noticeable in the anterior half of the living nearly mature larva. Before forming its puparium, a larva voids the gut contents and then releases the whitish calcium compound through the anus. By vigorous movements, the larva manages to cover itself with the moist material which subsequently hardens to form a whitish deposit over the surface of the puparium. The function of this material is unknown, but it is strongly hydrofuge and may serve to prevent wetting of the puparium in the damp leaf litter. Although larvae of *Pseudocalliope flaviceps* possess these glands, their puparia are not covered by a whitish deposit. Possibly the material is incorporated into the mud-fiber case formed by the mature larva shortly before it pupates.

Another morphological trait possessed by all 8 species examined in this investigation is a pair of protrusible lobes that arise from the perianal pad. When evaginated, these lobes project laterally and are slender and tapering. They are repeatedly extended during locomotion and probably are best considered as being ambulatory structures.

The cephalopharyngeal skeleton is of the generalized type found throughout the cyclorrhaphous Diptera having saprophagous larvae. Pharyngeal ridges are present and the mouthhooks, hypostomal sclerite, and pharyngeal sclerite are not fused to each other. The pharyngeal sclerite has an anterodorsal bridge, and slender parastomal bars are present. The hypostomal sclerite is basically H-shaped and possesses a narrow bridge. The epistomal sclerite lying above the anterior end of the hypostomal sclerite varies in shape but always seems to possess slender rami that project posteriorly. These rami are not connected to the anterior end of the parastomal bars as they are in the rather closely related family *Seiomyzidae* (Bratt *et al.*, 1969; Knutson and Berg, 1966). Paired ligulate and subhypostomal sclerites are present, and each is usually composed of slender rodlike structures. A dental sclerite, usually somewhat triangular in shape, is present below the posteroventral border of each mouthhook. The mouthhooks are rather simple structures and may possess accessory teeth or serrations along the ventral margin of the hook part.

The anterior spiracles of the third-stage larvae are quite diverse, varying in shape, length, and number of apical papillae. Variation within a genus, as shown by fig. 18 (*Minettia lupulina*) and fig. 23 (*M. lyraformis*), can be as great as that between genera, and it is



doubtful whether the anterior spiracles can have any diagnostic value except at the species level.

The posterior spiracles (fig. 82–89) of the mature larvae likewise seem to possess little diagnostic value at the generic level, as they are rather uniform in appearance. They differ between species somewhat in the degree of branching of the interspiracular processes, position and shape of the spiracular openings, and color of the spiracular tubes.

The posterior spiracular discs vary considerably in shape, distribution and size of the marginal tubercles, and ornamentation and can be used to distinguish among the species studied in this investigation. The number of marginal tubercles varies between 4 and 6. The tubercle shape ranges from low, broad mounds (*M. lupulina*, fig. 97) to slender, tapering structures (*Pseudocalliope flaviceps*, fig. 99).

Perhaps the best external morphological character for separating species lies in the arrangement, size, and shape of the spinules that are present on the dorsum and venter of the various segments. The spinules frequently form distinctive patterns that can be used to distinguish species.

Based on knowledge currently available, the cephalopharyngeal skeletons of the first-stage larvae offer the single best diagnostic character for separating the species of Lauxaniidae studied in this investigation. Unfortunately, however, their small size, lack of sclerotization, and close attachment to the surrounding integument makes taxonomic use of this structure difficult. Rather surprisingly, differences in the mouthhooks (e.g. position and number of accessory teeth) are more apparent in the first instars than they are in the older larvae. Probably the rather similar structure found in the mouthhooks and other cephalopharyngeal sclerites of the second and third instars is the result of morphological convergence arising from the utilization of a common food substrate by a diversity of species. Thus, the morphology of the cephalopharyngeal skeleton of the first instar may be more significant phylogenetically than that of more mature larvae.

#### ABBREVIATIONS USED IN FIGURES

A, antenna; AL, ambulatory lobe; ASl, anal slit; ASp, anterior spiracle; AT, accessory tooth; bp, basal part of mouthhook; DB, dorsal bridge; DC, dorsal cornu; DS, dental sclerite; DT, dorsolateral tubercle; ES, epistomal sclerite; FM, facial mask; HB, hypostomal bridge; hp, hook part of mouthhook; HS, hypostomal sclerite; IP, interspiracular process; LS, ligulate sclerite; LT, lateral tubercle; M, micropyle; m, membrane; MH, mouthhook; MP, maxillary palp; MR, middorsal ridge; Pa, papilla; PB, parastomal bar; PP, perianal pad; PR, pharyngeal ridge; PSp, posterior spiracle; PST, posterior spiracular tube; R, ramus; SB, spinule band; ShS, subhypostomal sclerite; SSc, spiracular scar; SSl, spiracular slit; StC, stigmatic chamber; Tr, trabeculae; VC, ventral cornu; VT, ventrolateral tubercle; W, window.

All measurements indicated by scale lines are in millimeters.

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EDITORIAL NOTE

Beginning with issue number 1, volume 78 (1976), the Proceedings of the Entomological Society of Washington will be published during the months of January, April, July, and October. This schedule will eliminate the difficulties of publishing an issue during the month of December, when the overburdened postal service, vacations, etc., occasionally cause a delay in publication that stretches over into the following year, and thus creates (particularly for taxonomic papers) confusion as to date of publication.